

1 **Estimating growth from sex ratio-at-length data in species with sexual size**
2 **dimorphism.**

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6 **Abstract**

7 Individual growth is one of main processes which drive the population dynamic and
8 stock productivity. Many fish have differential individual growth by sex. Growth is
9 affected by sexual development, which is frequently reached at different sizes in males
10 and females. Differences in growth per sex after maturity produce different patterns in
11 sex proportions-at-length in the population. If these patterns are the consequence of
12 changes in life history parameters, sex ratio-at-length data can be expected to contain
13 significant information on the population life history. In this paper I first explore how
14 post-maturity changes in life history may shape these patterns in sex ratio-at-length;
15 secondly I explore how these data may be used to estimate growth parameters and
16 finally I discuss how this information may be useful for stock assessment purposes. I
17 use European hake data and life history parameters to model expected sex ratios. The
18 results suggest that reproductive energy allocation leads to a lower growth rate in male
19 hakes than in females. Moreover the sex ratio-at-length may provide useful information
20 for estimating growth parameters in dimorphic species if additional information from
21 other sources is available. Finally, these data can easily be factored into stock
22 assessment models to help provide a better estimation of growth parameters and
23 mortality rates. This valuable, accurate and cheap biological information (sex ratio-at-

length) may play an important role in population dynamic models and stock assessment for species with sexual size dimorphism.

Keywords: individual growth; sex ratio; sexual dimorphism; stock assessment models; hake.

1. Introduction

Individual growth is one of main processes which drive productivity and population dynamics. Biological knowledge about individual growth is essential to perform fish stock assessments and to be able to give scientific advice for management decision-making. Stock assessment models deal with the individual growth in many different ways. In age-based models such as VPA (Megrey, 1989; Shepherd, 1999), individual growth is frequently factored into the model by assigning weights to age groups based on hard structures such as otoliths, scales, etc. When this is not possible due to difficulties in interpreting hard structures, as in the case of European hake (de Pontual et al., 2006; Piñeiro et al., 2007), there are two options: if information is scarce a biomass dynamic model (Punt and Hilborn, 1996) can be drawn up. In such models individual growth is not estimated directly; instead a population growth rate that considers individual growth, natural mortality and recruitment all together is estimated. If stock information is good enough, different variants of length-based models can be drawn up. Platforms able to develop this kind of model include GADGET (Taylor, et al., 2007) and SS3 (Methot and Wetzel, 2013). Examples of these two implementations have been used for European hake (ICES 2010). In these statistical models individual growth parameters such as von Bertalanffy model parameters (von Bertalanffy, 1957) may be estimated within the model using the data available, which mainly comprise length-frequency in catches or surveys, although other sources of growth information such as

tagging-recapture data may also be used (Maunder and Punt, 2013). The growth parameters are estimated in such a way that the observed length frequency in each time step can be explained by the population dynamic model. A common problem is that the same information (length distributions) is also used to estimate other model parameters such as recruitment, selectivity and fishing mortality. This might create problems of over-parameterisation, correlation between parameters and the usual difficulties in estimating too many parameters with a limited amount of information. For this reason, the aforementioned models for European hake (ICES, 2010) have set L_{∞} and only estimate k with the length frequency data.

This lack of data can be overcome with additional biological information. Kuparinen et al. (2012a) review ways of increasing biological realism in stock assessment models and conclude that scientists must go beyond the traditional assessment process and explore other information sources from other fields such as ecology, life history theory and evolutionary biology. Informative data are crucial in providing scientific advice. In fishery stock assessment “informative data” means those that lead to accurate estimates of abundance and reference points (Magnusson and Hilborn, 2007). Individual growth is a key datum in estimating population abundance and reference points; however, apart from age-length keys and tag-recapture data there is little additional information that could improve their estimation through length-based assessment models (Maunder and Punt, 2013).

Two important points not frequently addressed in stock assessment models are significant when individual growth data are sought. One is the impact of sexual development on growth and other life history traits, and the other (related to the first), is sexual dimorphism. Many fish species have indeterminate growth, which means that

they keep growing asymptotically after reaching adulthood. Indeterminate growth results from allocating less and less energy to growth and more to reproduction. Length at maturity affects the shape of the growth curve as a result of trade-offs between reproduction and growth (Czarnowleski and Kozlowski, 1998). The von Bertalanffy growth equation is an approximation of this growth process; however, its use has been criticised because it implies that the change in energy allocation after maturity does not influence the growth rate. Day and Taylor (1997) hold that growth models for indeterminate growth species should be specified by two different equations: a pre-maturity equation in which no energy is allocated to reproduction and a post-maturity equation where at least some energy is devoted to reproduction. Growth models of this kind are known as biphasic growth models (Quince et al., 2008), and they have been applied to explain the individual growth of numerous species (Alós et al., 2010a; Alós et al., 2010b; Porch et al., 2002).

Sexual size dimorphism (SSD) refers to different body sizes in adult sexes. SSD is very frequent in many fish species including plaice and most flatfish (Rijnsdorp et al., 2010) or Spanish mackerel, where females mature at a larger body size, grow at a slower rate and attain larger body sizes than males (Juan-Jordá et al., 2012). Hake is another species in which adult females have larger body sizes than adult males (Murua, 2010). If length-at-maturity is different in males and females, so might other traits be, such as growth and natural mortality. The differentiation of male and female reproductive strategies is expected to produce sex-specific optima for traits that affect longevity and ageing, often favouring a faster life strategy in males than in females (Bonduriansky et al., 2008). Fecundity selection favours larger females because fish fecundity increases isometrically with body weight (Stearns, 1992).

SSD species with different growth and mortality rates may produce a sex ratio-at-length that differs by 50%, with variable proportions depending on size (Marshall et al., 2006; Murua, 2010). Changes in growth after maturity and growth differences between males and females are the processes that shape the sex ratio-at-length. How these two processes interplay and produce different patterns in sex ratio-at-length is not well known and I have found no significant information on this issue in my review of the relevant literature. If sex ratios-at-length patterns result from different life history traits, the data can also be expected to contain information on growth and mortality. In European hake (*Merluccius merluccius*), males mature at a smaller sizes than females and also have smaller adult sizes than females (Murua, 2010). These different traits produce specific patterns in European hake sex ratio-at-length (Cervino et al., 2013). This pattern could be useful for stock assessment models if a quantitative link between life history and sex ratios can be found. In this paper I explore this link, first developing a model to help understand how post-maturity changes in growth and mortality may shape the sex ratio-at-length; secondly developing a likelihood function that compares the observed and modelled sex ratio-at-length so as to enable growth parameters to be estimated; and finally discussing how this information may be factored into stock assessment models so that better scientific advice can be offered.

2. Material and methods

I use two sources of information in this analysis: (1) sex ratio-at-length data from European hake; and (2) a length-based model that takes into account sexual differences in growth and mortality after maturity.

The sex ratio-at-length is presented in Figure 1. The left-hand panel shows the historic figures from 1982 to 2008, and the right-hand panel shows the mean for 3 years (2006-

08), which is used later as a reference for examining the sex ratios produced by the model. These data come from Spanish sampling (IEO and AZTI) in the Bay of Biscay area (ICES Division VIIIa, b, c, d) including commercial fishing (trawl gillnet and long liners) and surveys. Sex data on hake north of the Bay of Biscay are not available because the fleets that operate in those areas land the fish un-gutted. The sex ratios shown in Figure 1 begin with figures of around 0.5 for fishes at 20 cm. Length classes below 20 cm are more difficult to sex accurately and were not sexed in the sampling process. From 25-30 cm the proportion of females starts to decrease, and reaches its minimum at around 40 cm, where the female ratio may be as low as 0.1. From 40 cm to 60-70 cm the proportion of females rises progressively. Above 70 cm females account for 100% of the fish sampled. A similar pattern has been observed in recent years, although these extremely low historic proportions of females are never reached: the minimum ratio of females stands at slightly below 0.4.

Length-based model.

A length-based model is developed to reproduce hake dynamics. The model is sexed separately with a view to simulating the expected sex ratios under different life histories, considering different lengths at maturity, M and growth. These parameters may be different for pre-mature and post-mature fish, and also for post-mature males and females. The population is projected forward with constant recruitment, equal for males and females, until equilibrium is reached.

The different simulations are performed under different biological parameters that consider the current biological knowledge for males and females.

1. Pre-mature parameters (ICES 2010):

143 a. $k=0.165$;
 144 b. $L_{\infty}=130$;
 145 c. $t_0=0$;
 146 d. $M=0.4$.

147 2. Length at maturity (Murua, 2010; Dominguez-Petit et al., 2008):
 148 a. Males ~32 cm
 149 b. Females ~45 cm

150 3. Post-maturity: M , L_{∞} and k may take different values in males and females.
 151 Given the reproduction cost these values are constrained by the pre-maturity
 152 figures ($k<0.165$; $L_{\infty}<130$; $M>0.4$).

153 The population model follows a length based dynamic similar to that described by
 154 Taylor et al. (2007). The model works on a quarterly basis. The lengths range from 1 to
 155 130 cm. To compute the equilibrium population based on the equation below a fish
 156 population is started with a single recruit per year (0.5 males and 0.5 females) and
 157 simulated throughout its lifetime, applying the dynamics described in following
 158 equations, for a fixed level of fishing mortality, until the single initial individual is
 159 virtually extinguished due to mortality (i.e. when abundance is reduced to $1e-10$). In
 160 each quarter the sequential dynamic comprises 3 processes: recruitment, mortality and
 161 finally growth. The dynamic continues in the next quarter with the new recruitment.

162 Recruitment is apportioned equally on the first of May and the first of June, at the end
 163 of quarters 1 and 2, which are the main recruitment season (Mehault et al., 2010;
 164 Murua, 2010). Every year the recruitment abundance vectors for the four quarters are 0,
 165 0.5, 0.5 and 0. The recruitment length distribution has the following mean: $L_{\infty} * (1 -$
 166 $\exp(-k * 0.25))$ and a standard deviation of 2 truncated to lengths 1.5 to 19.5 cm.

The number of individuals in the population after mortality (N1) is given by:

$$(1) \quad N1_{t,l} = \text{Rec}_{t,l} * \exp(- (F_{t,l} + M_l) * 0.25)$$

where $N1_{t,l}$ denotes the population numbers at length at the start of a quarter t . M is the natural mortality and 0.25 is a the time step (quarter). Fishing mortality (F) is determined by a vector $F_{t,l}$, where $F_{t,l} = f_t * S_l$; with $S_l = 1 / (1 + \exp(-a*(l - L_{50})))$; where $L_{50}=27$; $a=0.2$. Subindex t stands for time (always quarters in this model) and l stands for length. N is the population abundance.

Expected growth follows a von Bertalanffy model with parameters L_{∞} and k with beta-binomial variability. The underlying idea is that an individual of length l grows according to the random variable:

$$(2) \quad \text{Growth}_l \sim \text{Binomial}(g_{\max}, p_l), \text{ where } p_l \sim \text{Beta}(\beta \alpha_l, \beta),$$

$$(3) \quad \text{with } \alpha_l \text{ chosen such that } E[\text{Growth}_l] = g_{\max} * \alpha_l / (\alpha_l + 1) = (L_{\infty} - l) * (1 - \exp(-k_l * 0.25)).$$

where β controls the amount of variability in growth, with larger values of β corresponding to lower variance in $\text{Growth}(l)$. The proportion of individuals in $N1_{t,l}$ that grow to length l' , denoted as $g_{l,l'}$, is given by the probability of the variable $\text{Growth}(l)$ taking the value $l' - l$ and can be explicitly written as a function of g_{\max} , L_{∞} , k and β ; where $g_{\max}=15$ and $\beta=4$ in all simulations and L_{∞} and k varies in different simulations.

The number of individuals of length l in the population after growth (N2) is given by

$$(4) \quad N2_{t,l} = \sum_{l' \leq l} (N1_{t,l'} * g_{l',l})$$

188 All population numbers after a new recruitment (N) is incorporated to the population are
 189 given by:

$$190 \quad (5) \quad N_{t,l} = N2_{t,l} + Rec_{t,l}$$

191 where Rec is the recruitment in the quarter with figures 0, 0.5, 0.5 and 0 over the four
 192 quarters. And the model loops continue in equation 1 until the population is virtually
 193 extinguished. N1, N2 and N refer to the 3 sequential processes in each quarter.

194 Equilibrium catch numbers (C) at length are given by the equation:

$$195 \quad (6) \quad C_{t,l} = N_{t,l} * (1 - \exp(-F_{t,l} * 0.25))$$

196 Notice that this catch equation, like the dynamic model equations, does not follow the
 197 cohorts. It is not the same as the classic Baranov equation. This F can not be interpreted
 198 in the same way: for instance it does not have the same additive properties, although it
 199 is a close approximation to the Baranov equation when the time step is reduced.

200 The model works with the sexes separated. Sex subindices (m and f) are not presented
 201 in previous equations for simplicity. The equations for estimating sex-related results are
 202 the following:

203 The female sex ratio-at-length (SexRat) is calculated by:

$$204 \quad (7) \quad SexRat_{l,f} = N_{l,f} / (N_{l,m} + N_{l,f})$$

205 A Least Square fit is developed to minimise differences between observed (Obs) and
 206 modelled (Exp) sex ratios to explore the options for estimating growth parameters from
 207 sex ratio-at-length. The Least Square score (LS) is:

208 (8) $LS = \text{sum}[(\text{Obs}(\text{SexRat}_{l,f}) - \text{Exp}(\text{SexRat}_{l,f}))^2].$

209 Operational sex ratios (OSR) refer to the ratio of individuals which are sexually active
 210 at a given time. The operational sex ratio in the population is estimated as follows:

211 (9) $OSR = \text{sum}[N_{l,f} * \text{Mat}_{l,f}] / (\text{sum}[N_{l,f} * \text{Mat}_{l,f}] + \text{sum}[N_{l,m} * \text{Mat}_{l,m}])$

212 Finally, as a support for the growth estimations, some figures for sex L_∞ are required.
 213 These are estimated following the Charnov (1993) life history invariants for the ratio of
 214 length at maturity (L_{mat}) to asymptotic length (L_∞). Charnov (1993) says that the ratio of
 215 L_{inf} to L_{mat} is relatively constant among similar species. To estimate male and female
 216 L_{inf} the aforementioned figures for length at maturity were used, along with the ratio
 217 $L_\infty / L_{\text{mat}}$ taken from different hakes all over the world as presented in FishBase
 218 (www.fishbase.org). The 19 records available provide a mean value for this ratio of 2.49
 219 and an s.e. of 0.20.

220 3. Results and discussion

221 3.1. How do growth and mortality affect sex ratio-at-length?

222 This section explores how different changes in life history parameters (k , L_∞ and M)
 223 after maturity may shape the sex ratio-at-length. In the absence of post-maturity changes
 224 in life histories the female ratio should remain at 0.5 for all lengths.

225 Figure 2 shows the impact of a change in L_∞ , k or M after maturity when males and
 226 females experience the same post-maturity figures. Males mature at 32 cm and females
 227 mature at 45 cm. This means that males change their life history figures before females.
 228 Reduction of L_∞ after maturity produces a decrease in the ratio of females (Figure 2.
 229 Left-hand panel). This decrease begins at 32 cm and is higher when the reduction of L_∞

is also higher. After reaching its minimum (0.3 with L_{∞} reduction from 130 cm to 50 cm), the female ratio increases to its maximum at around 50 cm. This increase is also higher and steeper when L_{∞} reductions are more noticeable. After reaching the maximum, the female ratio stabilises up to maximum length (130 cm). Reducing k after maturity produces patterns similar to those found when reducing L_{∞} . In both cases the modelled sex ratio is similar to the observed patterns (Figure 1). However, to reach similar figures, with 100% females for fish of 70 cm and longer, the growth reduction (L_{∞} or k) would have to be incredibly high. For instance, with a reduction of L_{∞} from 130 cm to 50 cm for mature males and females, the maximum ratio is never reached. 50 cm is an unrealistic L_{∞} for European hake, where females more than 100 cm long and males of around 60-70 cm are frequently found in commercial landings.

Figure 2 (right-hand panel) shows the impact of an equal (male and female) post-maturity M increase. In this case the pattern is totally different from the one described above for growth. When the male M increases (at 32 cm) the female sex ratio increases up to a size of 45 cm. At this size the female M also increases and becomes the same as the male M . Subsequently the female sex ratio stabilises with figures above 0.5. The higher the M increase, the higher the female sex ratio for larger fish is. However, although post maturity changes in M may shape the sex ratio-at-length, the M cannot by itself explain the sex ratios observed in Figure 1, because it never produces female figures below 0.5 after male maturity (32 cm).

Figure 3 presents the results of a simulation similar to those presented in Figure 2. However, by contrast with the previous simulation, in this case the changes in post-maturity parameters are different in males and females. Post maturity reductions in L_{∞} produce the female sex ratios presented in the left-hand plot. If the reduction in females

(from 130 to 90) is greater than the reduction in males (from 130 to 110 cm) the sex ratio decreases after male maturity, then increases until female maturity and then decreases again sharply (solid line). The pattern changes if the reduction in males is greater than that in females. In this case (dashed lines) the female sex ratio decreases after male maturity, then increases to 100% females. The size at which 100% females is achieved depends on the differences in L_{∞} reduction between males and females. The greater the differences, the smaller the size at which a ratio of 100% females is achieved. If growth reduction is simulated with changes in k (middle plot) the results are quite similar to those for the L_{∞} reduction. However, in this case a small proportion of males remains until the largest size is reached (130 cm). The sex ratio patterns are completely different if the post-maturity changes take effect at M . The reduction observed in the ratio of females after male maturity never happens. If the M increase is greater for females, then the female sex ratio tends towards zero for greater lengths. If the M increase is greater for males then the female sex ratio for large fish goes to 1.

This preliminary analysis shows some important features that reveal how changes in life histories after maturity may help to explain the sex ratios-at-length observed. First of all a post-maturity growth reduction is needed for a sex ratio pattern similar to those observed to be obtained. Furthermore, it is important for this reduction in growth to be more pronounced in males than in females. Changes in M may also alter the sex ratio-at-length, but they cannot by themselves explain the sex ratios observed.

3.2. Optimisation analysis.

An optimisation model is implemented to explore the usefulness of sex ratio-at-length data for estimating growth parameters. All the parameters that have an impact on the sex ratio at length must be considered, i.e. M , L_{∞} and k before and after maturity for

both sexes, making a total of 12 parameters. To avoid over-parametrisation problems, some additional information is needed to perform these simulations. L_{∞} and k for pre-mature individuals are set equal in male and females as in the ICES (2010) model ($L_{\infty}=130\text{cm}$; $k=0.165$ and $M=0.4$). Given the reproduction cost, these figures also act as a limit for the estimation of post-maturity parameters, with $L_{\infty}=130$ and $k=0.165$ being the upper limit for post maturity growth and with $M=0.4$ being the lower limit for post-maturity natural mortality. This approach enables the options for estimating growth with sex ratio-at-length data to be explored. However, some limitations are observed and an alternative approach is also proposed. This consists of reducing the number of parameters estimated and setting L_{∞} according to the ratio of maturity length to L_{∞} (Charnov, 1993). This ratio is calculated from additional data taken from different hake species in the FISHBASE database (www.fishbase.org). The estimated mean ratio is 2.5. Considering that males mature at 32 cm and females at 45 cm, this ratio makes L_{∞} 80 cm for males and 112 cm for females.

Figure 4 shows the least square fit for two options: with free L_{∞} and two different scenarios (left-hand panel) and with fixed L_{∞} and 3 different scenarios (right-hand panel). Table 1 shows the parameters for each of these 5 scenarios (Sce. 1 and 2 for free L_{∞} and Sce. 3, 4 and 5 for fixed L_{∞}) with the corresponding least squares scores. The symbol “*” in Table 1 indicates which parameters are estimated in each scenario.

The left-hand plot (Figure 4) shows the model fit for the four post-maturity growth parameters, i.e. L_{∞} and k for males and females (solid line). Female L_{∞} and k and male k remain the same as in the pre-maturity levels. Male L_{∞} is reduced from 130 cm to 66.5 cm with an LS score of 0.150. If male M and L_{mat} (length at maturity) are also

estimated, these values increase from 0.4 to 0.44 (M) and from 32 cm to 33.2 cm (Lmat). The corresponding LS score is reduced from 0.15 to 0.129.

The right-hand plot (Figure 4. Solid line) shows that the post-maturity L_{∞} reduction (from 130 cm to 112 in females and from 130 to 80 cm in males) approaches the observed values with $LS=0.50$ (Table 1. Sce. 3). In this case no parameters are estimated. This fit may be improved if the values of k for males and females are also estimated (dashed line). In this case female k does not change and male k is reduced from 0.17 year⁻¹ to 0.11 year⁻¹ (Table 1. Sce. 4). This male post-maturity k reduction brings the LS score down from 0.50 to 0.189. This fit may also be improved if male M and male Lmat (length at maturity) are also estimated (dashed line). In this case the LS score is reduced from 0.189 to 0.161 (Table 1. Sce 5). The corresponding M and Lmat figures are 0.45 and 33.1 cm. The best fit is obtained with a greater reduction in growth among males and a greater increase in M compared with the figures for females. These results are consistent with a higher cost of reproduction for males than females.

The system presented here to estimate growth based on the sex ratio-at-length has certain limitations. Firstly, the sex ratio-at-length is influenced by many different parameters (L_{mat} , M , k and L_{∞}), and those parameters differ for males and females. Different combinations of them may provide similar fits, making it hard to estimate growth. However, once these limitations are taken into consideration, the exercise performed is still useful in helping to understand how the cost of reproduction may affect the growth of males and females differently. In most scenarios the female parameters are constrained at the limit of the range, while the male parameters are estimated to get the best fit. This indicates the value of these data in relative terms, i.e. different combinations of the same parameter, such as L_{∞} for both sexes, may result in

similar fits. To solve this situation additional information may be useful. Here the model fit is explored setting L_{∞} for both sexes based on life history invariants (L_{∞}/L_{mat} ratio). This constraint provides more realistic results and also provides a better estimation of other parameters. The fit without this constraint is female $L_{\infty}=130$ and male $L_{\infty}=66.5$ cm, with these differences between males and females being much bigger than expected. Moreover, in this case k does not change since the cost of reproduction in terms of growth is only charged to L_{∞} by the model. With post-maturity L_{∞} based on life history invariants, the model charges the cost of reproduction in terms of growth to both parameters (L_{∞} and k). In both cases the increase in post-maturity M is also a cost of reproduction. Differences in natural mortality for the different sexes have also been observed in other hake species where males have a higher M than females (Gatica and Cubillos, 2004) and in summer flounder (Maunder and Wong, 2011).

The importance of the survival cost of reproduction has received little attention in fishery assessment models. This cost arises from the energy allocated to reproduction, e.g. gonad development and egg production, and to reproductive behaviour, e.g. increased risk of being caught or a loss of efficiency in foraging (Kuparinen et al., 2012b). The simulations performed here show that there is information in sex ratio-at-length data that enables post-maturity M to be estimated. This estimation is more accurate if additional information on other parameters and constraints on those parameters can be set according to ecological knowledge. The models drawn up also show that males, which have a relatively higher survival cost than females, help to explain the sex ratio observed. The lack of knowledge of the reproductive behaviour of hake makes difficult to figure out why males have a higher reproductive cost than females. However, it has been observed that hake caught by gillnetters and long-liners in the reproductive areas and seasons are mainly females. The presence of hydrated eggs

in these females is evidence that males are also present. Gillnets catch fish that are moving and long-lines catch fish that are eating. Male reproductive behaviour involving reduced movement and reduced food intake might explain the higher reproductive cost of males.

The negative correlation between k and L_{inf} is also a known life history invariant (Charnov and Berrigan, 1993). Estimating a value for this parameter based on similar populations or species might also help to reduce the over-parameterisation problem and help to better estimate growth parameters.

3.3. Impact of fishing on sex ratios

Finally, some simulations with different fishing mortality (F) values are presented in figure 5 to explore the impact of F on sex ratios. The biological parameters for this exercise are those of Sce. 5 in Table 1. The model is an equilibrium model implemented on a “per-recruit” basis. This means that the population is projected forward with constant recruitment (1 individual) until equilibrium is reached. F_{max} is the level of F that produces the maximum catch in equilibrium. The model is run with 3 different F levels: $F=0$ means that there is no fishing; F_{max} means that F is at the level that produces the maximum catch; and $2 \cdot F_{max}$ means that F is twice the level that produces the maximum catch. This last level may be considered as overexploitation. In all previous simulations the F level was set as $2 \cdot F_{max}$, which is in consonance with the actual exploitation levels in 2006-08.

Figure 5 (upper plot) shows how the modelled sex ratio-at-length changes under different fishing intensities. With no fishing (continuous line) the presence of females is relatively lower between 32 and 80 cm. with a minimum around 0.3 at 37 cm and a

maximum at 80 cm. When the fishing mortality increases, the minimum shifts from 0.3 (F=0) to 0.36 at $2 \cdot F_{\max}$, and the maximum is reached at a lower size: 70 cm ($2 \cdot F_{\max}$), compared to 80 cm (F=0). The middle plot shows how the increase in F changes the population structure by truncating the larger size classes. In the absence of fishing (F=0), fish larger than 70 cm are relatively abundant. Since most of these large fish are females, when F increases and truncates the population to a lower size the number of large females may be expected to decrease. So although F is not sex selective in the model, it has an impact on the sex ratio and also on the reproductive success of the population. To better illustrate this idea, the lower plot in Figure 5 shows how the increase in F alters the operating sex ratios (OSR). OSR refers to the ratio between the number of mature females and total mature fish (males and females). In the absence of fishing the OSR in the population is 0.44. This is because males mature at a smaller size (32 vs. 45 cm) and because the higher post-maturity male M (0.45 vs. 0.4) is not enough to counteract the smaller maturity size. Differences in growth do not affect OSR but the different sizes of mature males and females. As explained above, when F increases the proportion of males also increases because of the truncation of the large size population. Thus, at F_{\max} OSR decreases to 0.35 and under overexploitation ($2 \cdot F_{\max}$) the female sex ratio is 0.28. This strong decrease in OSR may have an important impact on the reproductive success of the population. Models that not consider sexual size dimorphism may ignore the risk associated with the loss of large females.

The simulations performed here show that sex ratio-at-length patterns are also affected by fishing mortality. This means that changes over time in sex ratios might help to understand changes in F, making these data valuable for assessment purposes. The consideration of time series of sex ratio data in fishery stock assessment models is simple in the Integrated Analysis framework (Maunder and Punt, 2013).

It has been determined that the proportion of females in the mature population decreases when fishing increases. This is true under the assumption that fishing mortality is only size dependent. If fishing mortality is also sex dependent the results might change depending on which sex has higher catchability. If the assumption is correct this may have implications for fishery management in terms of defining biomass reference points or diagnosing stock status. Fishing mortality truncates larger length classes. As females are larger than males, females are especially truncated, thus decreasing the reproductive potential of the population and its resilience in a changing environment (Hidalgo et al., 2012). This effect may be exacerbated if female fecundity per weight increases with size as is the case in hake (Mehault et al., 2010; Cerviño et al., 2013)

4. Conclusions

Changes in growth after maturity explain the shape of the sex ratio-at-length curve. Males mature smaller than females. The reduction on post-maturity growth among males increases the proportion of males at post-maturity sizes. This proportion is balanced at larger sizes due to the relative growth reduction in males. Then females mature and their growth are also reduced. If growth reduction among females is the same as among males then the sex ratio for sizes larger than the length of females at maturity stabilises with a higher proportion of females, although a figure of 100% females is never reached. For this to happen the growth reduction must be greater in males than in females. Changes in post-maturity mortality also result in the sex ratio shifting away from 50%, but those changes cannot by themselves explain the sex ratios observed. Sex differences in growth are the main factor that explains the shape of the sex ratio-at-length.

European hake is an important commercial species with unknown growth, which makes it more difficult to provide scientific advice on its management. The use of sex ratio-at-length data is a novel approach that helps provide a better understanding of hake growth, where trade-offs between reproduction and growth are explained, which contributes to a better implementation of the ecosystem approach to fisheries. The exercise presented here shows the utility of sex ratio-at-length for estimating growth in SSD species. Other factors such as length at maturity and mortality may also help to explain patterns in sex ratio-at-length. Since not all the parameters that explain the sex ratio data can be estimated at the same time, the method presented here may be useful for estimating growth parameters if additional information is available. That additional information could be the figures for one or more known parameters such as length at maturity or life history theory, which may help to keep the relationships between parameters within credible boundaries (Beverton, 1992; Charnov, 1993).

The most promising application of sex ratio-at-length is in integrated stock assessment models (Maunder and Punt, 2013). These data can easily be factored into models separated by sex merely by adding a new likelihood function that compares observed and modelled sex ratios-at-length. This novel source of information may help to estimate F, M and growth parameters throughout the time series of such models. Sex ratio-at-length is cheap information and long time series data are available for most fish stocks. In SSD species where there are differences in growth and reproduction, this information enables the assessment process to be improved so that better parameter estimation is obtained.

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Table 1. Optimization scenarios with different estimated parameters. Sce 1 and 2 represent optimization scenarios where Linf is also estimated. Sce3, 4 and 5 represent optimization scenarios where Linf is set based in hake correlation among length at maturity and Linf. The symbol * indicates which parameters were estimated. M, Linf and k are the parameters before maturity (equal for males and females); Lm is the length at maturity; M2, Linf2 and k2 are the post maturity parameters, different in males and females. LS is the Least Square value for every optimization scenario.

	Sce1		Sce2		Sce3		Sce4		Sce5	
	fem1	mal1	fem2	mal2	fem3	mal3	fem4	mal4	fem5	mal5
M	0.4	0.4	0.4	0.4	0.4	0.4	0.4	0.4	0.4	0.4
Linf	130	130	130	130	130	130	130	130	130	130
k	0.165	0.165	0.165	0.165	0.165	0.165	0.165	0.165	0.165	0.165
Lm	45	32	45	33.2 *	45	32	45	32	45	33.1 *
M2	0.4	0.4	0.4	0.44 *	0.4	0.4	0.4	0.4	0.4	0.45 *
Linf2	130 *	66.5 *	130	66.5	112	80	112	80	112	80
k2	0.165 *	0.165 *	0.165	0.165	0.165	0.165	0.165 *	0.11 *	0.165	0.11
LS	0.15		0.129		0.500		0.189		0.161	

Figure 1. Female proportion-at-length for a time series from 1984 to 2008 (left panel) and mean of recent years, from 2006 to 2008 (right panel) in the Gulf of Biscay.

Figure 2. Impact of post-maturity change in life histories (L_{inf} , k and M) on modelled sex ratio-at-length. The three plots show the same post-maturity changes in males and females. Vertical dashed lines represent the length-at-maturity for males (32 cm) and females (45 cm). Left panel shows the impact of reduced L_{inf} after maturation; middle panel shows the impact of reduced k after maturation; right panel shows impact of increased M . Pre-maturity figures ($M=0.4$; $L_{inf}=130$ and $k=0.165$) have been modified after maturity following the plot labels.

Figure 3. Impact of post-maturity change in life histories (L_{inf} , k and M) on modelled sex ratio-at-length. The three plots show different post-maturity changes in males and females. Vertical dashed lines represent the length at maturity for males (32 cm) and females (45 cm). Left panel shows the impact of reduced L_{inf} after maturation; middle panel shows the impact of reduced k after maturation; right panel shows impact of increased M . Pre-maturity figures ($M=0.4$; $L_{inf}=130$ and $k=0.165$) have been modified after maturity following the plot labels, that show first the new male value, and second the new female value.

Figure 4. Least square fit for two different approaches. The left plot shows the model fit estimating post-maturity L_{inf} plus k in males and females (continuous line) and two more parameters, i.e. male M and male L_{mat} (dotted line). The right plot shows the model fit for three different scenarios with fixed L_{inf} for females (112 cm) and males (80 cm). The continuous line shows the modelled results where L_{inf} was set (112 cm and 80 cm). Dashed line shows the fit where k (males and females) are also estimated. Dashed line shows the fit based in the previous plot fit plus two more parameters (male length at maturity and male M) which are also estimated.

Figure 5. Impact of different fishing levels ($F=0$; $F=F_{max}$ and $F=2 \cdot F_{max}$) on the sex ratio. Upper plot shows the impact on sex ratio-at-length. The middle plot shows the impact on equilibrium sex distribution. Lower plot shows the impact on operational sex ratios. X axis values are the three aforementioned F values.

Figure 1:

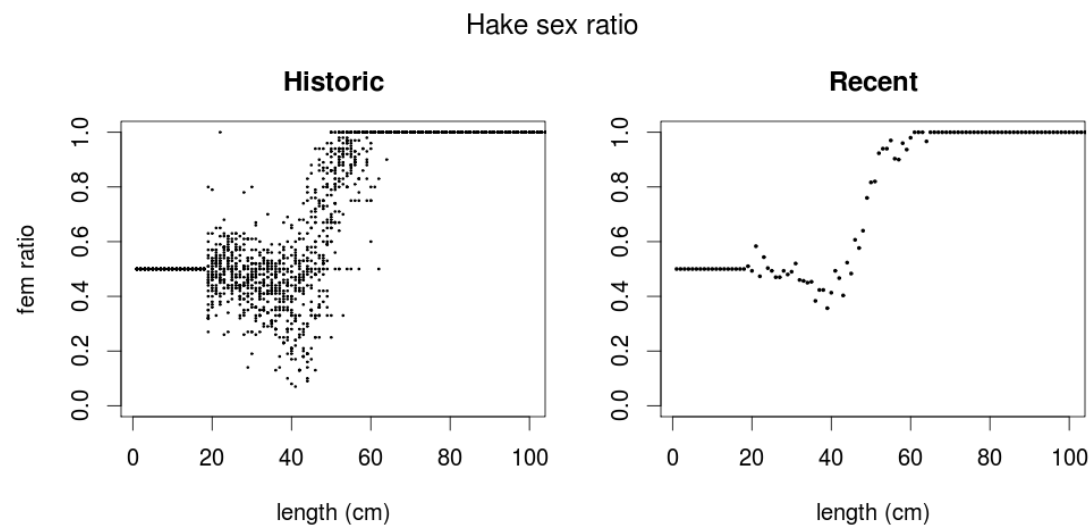


Figure 2:

Equal change in males and females after maturity

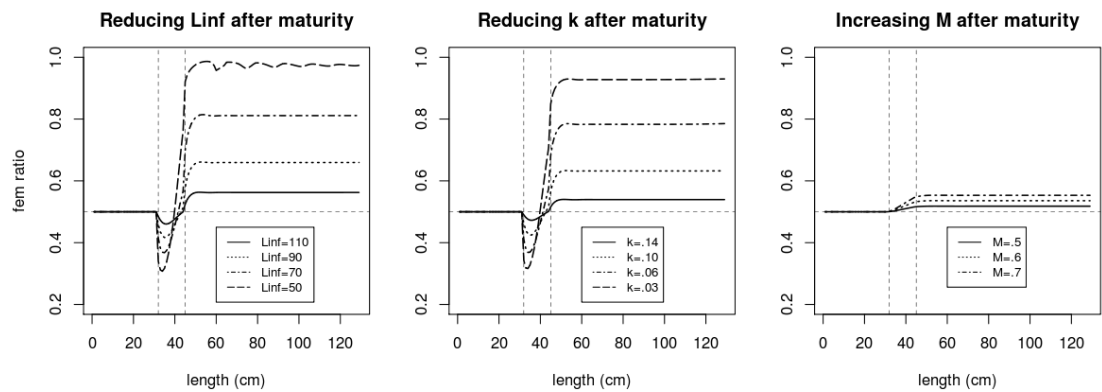


Figure 3.

Different change in males and females after maturity

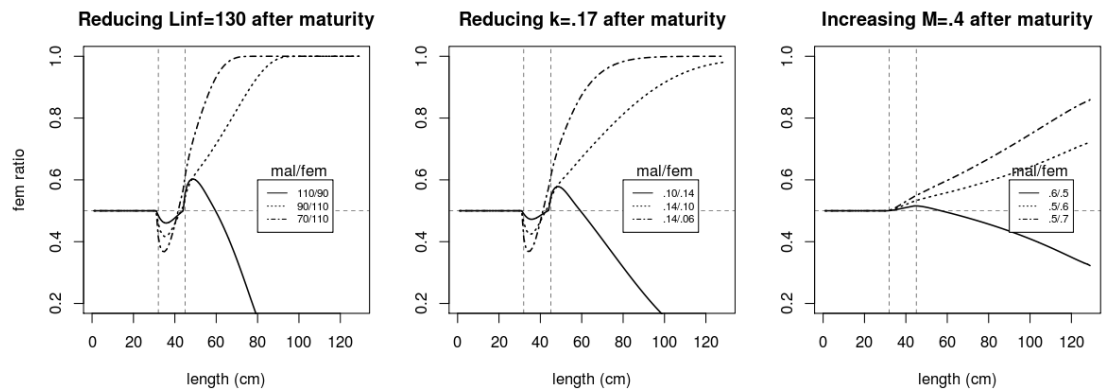


Figure 4.

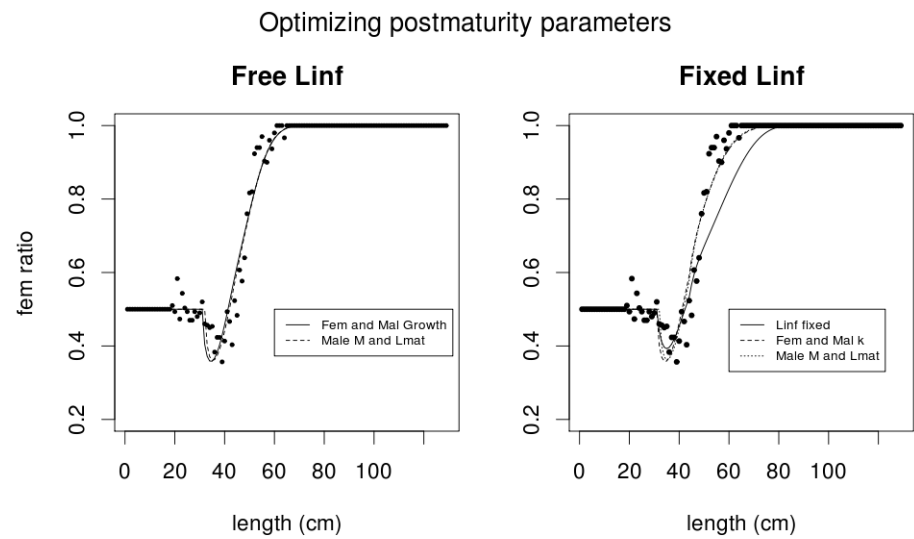


Figure 5.

impact of F on sex ratio

